

## NEW COMBINATIONS IN *SWERTIA* (GENTIANACEAE)<sup>1</sup>

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Several problems of generic delimitation in the Gentianaceae, tribe Gentianeae, remain inadequately investigated. Interim decisions on generic treatments are, however, required for the revised edition of the *National List of Scientific Plant Names*, to be published by the Soil Conservation Service, United States Department of Agriculture, and the Department of Botany, Smithsonian Institution (target date 1979). The present paper includes a review of studies to date bearing upon the question of whether *Frasera* Walt. should be accepted as a genus distinct from *Swertia* L., and explains my reasons for including *Frasera* in *Swertia* in the forthcoming *National List*.

Subsequent to St. John's (1941) summarization of the case for including *Frasera* in *Swertia* (following several earlier authors), more recent data on chromosome numbers have led some authors to favor the retention of *Frasera*. Hitchcock (1959) accepted *Frasera* as a genus with  $x = 13$  and *Swertia* s. str. with  $x = 9, 12$ , and  $14$ , largely on the basis of an unpublished thesis by D.M. Post in 1950. (Post's cytotaxonomic conclusions had been based on data published by Rork in 1949; Hitchcock evidently also consulted Darlington & Wylie's [1957] compilation, since no multiple of  $14$  was reported until 1952.) *Frasera* was said to differ further in having tetramerous flowers and a distinct, slender style  $2$  mm or longer, contrasting with pentamerous flowers and a short, poorly differentiated style or no style in *Swertia*. *Swertia* was described as consistently having opposite or alternate rather than whorled leaves, two distinct foveae on each corolla lobe, and completely separate stamens without crown scales; *Frasera*, however, was said to be variable in having either opposite or whorled leaves, paired or solitary foveae, and stamens either separate or connected by a crown, the crown if present bearing well-developed, rudimentary, or no scales between the filaments. Allred (1977) followed Hitchcock (1959); further distinctions pertaining to stature, presence or absence of rhizomes, corolla color, and habitat evidently were intended only to the Utah representatives of this complex, since even the western North American species placed in *Frasera* by Card (1931) and Hitchcock (1959) are variable in these respects. Threadgill & Baskin (1978) concentrated only on *Swertia caroliniensis* (Walt.) O. Ktze. (as *Frasera caroliniensis* Walt.), with the objective of determining with which of the western North American groups, respectively designated *Frasera* and *Swertia* by Post, this eastern species was affiliated. Their acceptance of *Frasera* was based largely on Post's work (an unpublished dissertation in 1956), with the addition of Stout & Balkenhol's (1969) biochemical studies, discussed below.

Toyokuni (1956) expanded *Frasera* to include *Ophelia* D. Don of eastern Asia. *Frasera* sensu Toyokuni thus comprised species then known to have  $x = 10$  as well as  $x = 13$ . He rejected most of the morphological distinctions, however, recognizing *Frasera* almost entirely on the basis of chromosome numbers.

The North American species treated as *Frasera* do differ from *Swertia perennis* L., the only North American species of *Swertia* s. str., much as Hitchcock (1959) and Threadgill & Baskin (1978) stated, except for inconsistencies in the stylar character, already noted by St. John (1941) and several earlier authors. Such species as *S. caroliniensis*, *S. pahutensis* (combination published below), and *S. radiata* (Kellogg) O. Ktze. are obviously closely related to each other, and more distantly related to *S. perennis*. On the other hand, such North American species as *S. albicaulis* (Dougl. ex Griseb.) O. Ktze. and *S. fastigiata* Pursh (chromosome numbers unknown), although they do exhibit the traits ascribed to *Frasera* by these authors, resemble *S. perennis* in their blue corollas and in their habit, being of low stature with most of the leaves basal, the cauline leaves being widely separated

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and those in the inflorescence greatly reduced.

As Toyokuni (1965) observed, however, the correlation among morphological traits breaks down when species from other continents are considered. Several species with pentamerous flowers have only one fovea per corolla lobe, e.g., *S. cordata* Wall. ex C.B. Clarke (Himalaya), *S. kilimandscharica* Engl. (eastern Africa), and *S. schimperii* (Hochst.) Griseb. (eastern Africa). Card (1931) illustrated foveae ranging from two distinct foveae per lobe through various degrees of fusion to one unlobed fovea, indicating a continuum of variation rather than two distinct categories. In *S. atroviolacea* H. Sm. (China), various degrees of fusion of the foveae can be found on a single specimen (Smith, 1936). *Swertia swertopsis* Makino (Japan) combines pentamerous flowers with a well-developed, slender style. The corolla lobes of *S. bimaculata* (Sieb. & Zucc.) C.B. Clarke (eastern Asia) are similar in size and shape to those of North American species placed in *Frasera*, but its flowers are pentamerous. Axis type was mentioned by Threadgill & Baskin (1978, following Post, ined.), but the limitations of its taxonomic value are evident from Card's (1931) and Toyokuni's (1963) discussions of the diverse types of inflorescences found in this complex. Both *S. albicaulis* (western North America, treated as *Frasera*) and *S. perennis* have slender inflorescences, with the pedicels arising directly from the main axis, whereas *S. macrosperma* (C.B. Clarke) C.B. Clarke and *S. pulchella* Buch.-Ham. ex D. Don (both Himalaya), both with pentamerous flowers, have diffuse, compound, much-branched inflorescences resembling those of the tetramerous-flowered *S. tetrapetala* (eastern Asia). Still greater diversity has been described in more recent years, as in *S. acaulis* H. Sm. (Nepal), in which the stem is only 1-2 cm long and the cyme divisions obsolete, the long pedicels appearing to arise from the caudex. Finally, one may note the pronounced similarity of *S. perennis* and *S. pseudochinensis* Hara (Japan) as illustrated by Toyokuni (1965; the latter species as *Frasera pseudochinensis* (Hara) Toyokuni), compared with the diversity among the species he assigned to *Frasera*.

Post's (1958) studies of nodal anatomy were interpreted by him and by Threadgill & Baskin (1978) as supporting the recognition of *Frasera*. Post, however, reported five, rather than two, major types of nodal anatomy among the North American species, and found some species, especially *Swertia perennis*, to be remarkably variable even within individuals. Since no taxa from other continents were studied, the taxonomic significance of nodal anatomy in the complex as a whole cannot yet be assessed. Lindsey (1940) studied the floral anatomy of several species in this complex, but did not indicate which he accepted as *Swertia* and which as *Frasera* except for *S. perennis* L. and *F. speciosa* Dougl. ex Hook. [= *S. radiata* (Kell.) O. Ktze.]. However, he commented only upon the similarities among all of these species, particularly in the placentation and in the branching of the main corolla traces below the separation of the corolla tube from the receptacle.

Nilsson's (1967, 1970) studies of the pollen morphology of 53 taxa in *Swertia* s. lat. disclosed the existence of several types of pollen grains, but pollen morphology was not well correlated with the sections into which *Swertia* s. lat. had been divided by Gilg (1895). Nilsson followed Gilg (1895) in accepting the broad concept of *Swertia*, including *Frasera* and *Ophelia*. In his 1970 paper, however, he noted the relative uniformity in pollen morphology among the North American species exclusive of *S. perennis*, and suggested that this might support their treatment as a separate genus, along with *S. tetrapetala*, which has similar pollen, and possibly some other eastern Asiatic species. This suggestion would not be equivalent to Toyokuni's (1956) inclusion of all of *Ophelia* in *Frasera*; some species treated as *Ophelia*, including the other Japanese taxa studied by Nilsson, have dissimilar pollen. One of the Asiatic species with pollen similar to that of the North American species is *S. acaulis* H. Sm. (Nepal), which corresponds well to recent concepts of *Frasera*. It is, however, according to Smith, (1970), a part of the *S. hookeri* C.B. Clarke complex, which comprises species "all obviously of close affinity," yet at least some other members of this group do not possess this type of pollen. Conversely, pollen of similar appearance is known from some species, such as *S. handeliana* H. Sm. (eastern Asia), with pentamerous flowers and other traits of *Swertia* s. str.

It is unfortunate that recent authors have cited the supposed differences in chromosome number

believed by Post and Hitchcock, from the few counts published through 1955 ( $x = 13$  then known from only one species in the whole complex!), to separate *Frasera* from *Swertia*, without reference to more recent counts. Those now available indicate a much more complicated situation, including  $n = 8, 9, 10, 12, 13, 14, 21$ , and 39. Also, even allowing for the possibility of an occasional error, it is evident that dysploid chromosome numbers sometimes occur within species; four of the species reported to have  $n = 13$  are also reported to have  $n = 12$ , and still other counts have been published for two of these. (For compilations of chromosome counts, see Toyokuni, 1965; Bolkhovskikh et al., 1969; Moore, 1973; and Vasudevan, 1975.) From this array of chromosome numbers, it is difficult, in the absence of strong support from morphology (see discussion below), to attach special significance to  $x = 13$  either alone or in combination with  $x = 10$ , much less to suggest that taxa with  $x = 13$  are more closely related to *Gentiana* than to the rest of the *Swertia* complex.

According to Vasudevan (1975),  $n = 13$  is the most frequently encountered chromosome number in *Swertia* s. lat. It is found in North America, Asia, and Africa, in diverse species that have been assigned to different sections or segregate genera. Chromosome numbers published since 1955 clearly demonstrate that the basic number 13 is by no means exclusively correlated with the traits attributed to *Frasera* by Post, Hitchcock, and Threadgill & Baskin. For example, *S. petiolata* Royle ex C.B. Clarke and *S. thomsonii* C.B. Clarke (both Himalaya; both  $n = 13$ ) correspond strictly to their concept of *Swertia*, being of relatively low stature and similar to *S. perennis* in habit, and having pentamerous, deep blue corollas, two foveae per corolla lobe, and sessile stigmas. *Swertia cordata* ( $n = 13$ ) corresponds to *Swertia* sensu these American authors in its pentamerous corollas but to *Frasera* in its monocarpic life cycle, solitary foveae, distinct style, and filaments "obscurely connate" at the base (fide Clarke, 1883). Several species with  $n = 13$ , e.g., *S. kilimandscharica* and *S. petiolata*, have pollen unlike that of the species that Nilsson (1970) suggested might be segregated as *Frasera*.

Stout & Balkenhol (1969; see also Stout, Christensen, et al., 1969) concluded that their comparative studies of xanthones supported the recognition of *Frasera*. Although they found significant differences between the species they treated as *Frasera* and those they accepted as *Swertia*, they also found major differences among species-groups within *Frasera*. Moreover, Stout et al. uncritically accepted as *Swertia* all species that had been so designated in studies of xanthones by other authors; thus among the *Swertia* species from which *Frasera* was said to be differentiated they included *S. chirayita* (Fleming) Karsten (sometimes called *S. chirata* Wall., nom. nud.) (Himalaya).<sup>2</sup> In general aspect, *S. chirayita* bears a greater resemblance to North American species placed in *Frasera* than to *S. perennis*, and it corresponds to American authors' delimitations of *Frasera* in having  $n = 13$ , tetramerous, yellowish corollas, and stamens connected by a crown. It also falls within Toyokuni's (1965) concept of *Frasera*, having previously been placed in *Ophelia*.

In later studies of xanthones, Jossang et al. (1973) were able to state that, among the species studied, only *Frasera* had xanthones substituted at positions 2 and 4, and all xanthones of *Swertia* were substituted at position 8. Conversely, however, some samples of *Frasera* lacked xanthones substituted at 2 and 4, and some did contain xanthones substituted at 8. This study was likewise limited in taxonomic applicability by the small number of species studied. Also, all of the Asiatic species studied, including *S. chirayita*, were accepted as *Swertia*, without reference to the fact that some had been treated as *Frasera* by Toyokuni and as *Ophelia* by other authors. The numerical-taxonomic representation of the xanthone data placed *Swertia* much closer to *Gentiana* than to *Frasera*, just the reverse of the cytotaxonomic conclusions of Post (in Hitchcock, 1959), and likewise too much at variance with morphology to be accepted as an indication of phylogeny.

<sup>2</sup>Stout et al. studied only species that they accepted as *Frasera*. The xanthones of these species were contrasted with those of *Swertia* species studied by other authors; the names of these species can be found in references cited by Stout et al.

Still later studies of the xanthones of *Swertia bimaculata* led Ghosal et al. (1975) to a contrasting emphasis in interpreting the taxonomic significance of these compounds. Xanthones of the types previously associated both with *Frasera* and with *Swertia* s. str. were found in this species, their data on xanthones thus tending to unite rather than to differentiate between these groups.

It is obvious that further studies of the *Swertia* complex, including species previously placed in *Swertia* s. str., *Frasera*, *Ophelia*, and *Lomatogonium* A. Br., considering diverse lines of evidence, and involving species from all parts of the range of this complex, will be necessary before a satisfactory delimitation of genera can be reached. For the present, however, arguments for the acceptance of *Frasera* seem inadequate, and arguments for the broader concept of *Swertia* seem sounder. Nor is there a question of maintaining nomenclatural ability; both *Frasera* and *Swertia* s. lat. can be found in currently standard North American floras.

It seems desirable, therefore, to make a name in *Swertia* available for the one North American species described in *Frasera* since St. John's (1941) revision:

SWERTIA PAHUTENSIS (Reveal) Pringle, comb. nov. Basionym: *Frasera pahutensis* Reveal, Bull. Torrey Bot. Club 98:107. 1971.

Also, some taxa treated as species by St. John (1941) were reduced or restored to varietal status by Hitchcock (1959). Since varietal status for these taxa has been widely accepted, the appropriate combinations in *Swertia* are hereby provided:

SWERTIA ALBICAULIS Griseb. var. COLUMBIANA (St. John) Pringle, comb. nov. Basionym: *Swertia columbiana* St. John, Amer. Midl. Naturalist 26:22. 1941.

SWERTIA ALBICAULIS Griseb. var. CUSICKII (A. Gray) Pringle, comb. nov. Basionym: *Frasera cusickii* A. Gray, Proc. Amer. Acad. Arts 22:310. 1887.

SWERTIA ALBICAULIS Griseb. var. IDAHOENSIS (St. John) Pringle, comb. nov. Basionym: *Swertia idahoensis* St. John, Amer. Midl. Naturalist 26: 24. 1941.

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